

A NEW SPECIES OF *CARPOCRISTES* (MAMMALIA: PRIMATOMORPHA)  
FROM THE MIDDLE TIFFANIAN OF THE BISON BASIN, WYOMING,  
WITH NOTES ON CARPOLESTID PHYLOGENY

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## ABSTRACT

A new species of Carpolestidae, *Carpocristes rosei*, is described from a middle Tiffanian locality in the Bison Basin, Fremont County, Wyoming. A phylogenetic analysis of all known carpolestid species identifies *C. rosei* as the most basal member of *Carpocristes*, a genus known from Tiffanian localities in North America and the Bumbanian Wutu Formation, Shandong Province, People's Republic of China. Available biostratigraphic and phylogenetic data suggest that *Carpocristes* originated in North America.

As reconstructed here on the basis of dental characters, phylogenetic relationships among carpolestids as a whole are highly compatible with the stratigraphic distributions of individual species. Nevertheless, stratigraphic disjunctions between inferred sister taxa imply ghost lineages that lasted roughly 5.6 Ma (for early members of the chronolestine clade), 2.3 Ma (for early members of the lineage culminating in *Elphidotarsius wightoni*), and 1.2 Ma (for early members of *Carpocristes*), respectively.

KEY WORDS: Paleocene, Carpolestidae, Phylogeny, Paleobiogeography

## INTRODUCTION

The Carpolestidae are a family of plesiadapoid primatomorphs characterized by pronounced specializations of the posterior premolars (Rose, 1975). All carpolestid taxa other than *Chronolestes simul*, for which the monotypic subfamily Chronolestinae has been erected (Beard and Wang, 1995), possess a bladelike or "plagiaulacoid" P<sub>4</sub> that occluded with equally specialized, polycusate P<sup>3-4</sup> (Biknevicius, 1986). With some notable exceptions (Fox, 1984), these highly derived posterior premolars became progressively elaborate through time (Rose, 1975, 1977), and their morphology has formed the principal basis for reconstructing phylogenetic relationships within the group (Rose, 1975; Krause, 1978; Fox, 1984; Beard and Wang, 1995; Bloch and Gingerich, 1998).

Carpolestids are fairly common components of North American Paleocene mammal faunas, where they range in age from late Torrejonian (To3) to late Clarkforkian (Cf3) (Archibald et al., 1987). Recently, the first Asian carpolestids were described from the Wutu Formation in the Wutu Basin, Shandong Province, People's Republic of China (Beard and Wang, 1995). One of these Asian carpolestids, *Carpocristes oriens*, is morphologically very similar to North American *Carpocristes hobackensis* and *Carpocristes cygneus*, and all three of these species are thought to form a clade within Carpolestidae. This particular clade is interesting not only because of its widespread geographic distribution, but also because it appears to document a relatively rare example of the successful invasion of Asia by an endemic North American mammal (Beard and Wang, 1995; Beard, 1998).

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The purpose of this paper is to describe a new species of *Carpocristes* from the Bison Basin in south-central Wyoming. This new species, the oldest and most primitive yet known for the genus, further substantiates the North American origin of *Carpocristes*. It also suggests that carpolestids enjoyed their highest species richness during the middle Tiffanian, when at least three species—*Elphidotarsius wightoni*, *Carpodectes hazelae*, and the new species of *Carpocristes* described below—are known.

Paleocene mammals from outcrops of the Fort Union Formation in the Bison Basin of south-central Wyoming were first reported by Gazin (1956). Additions and emendations to the Paleocene mammalian faunas of the Bison Basin have been made by McGrew and Patterson (1962), MacIntyre (1966), Van Valen (1966, 1978), Szalay (1973), Gingerich (1976, 1983), Sloan (1987), Gunnell (1989), and Thewissen (1990). Carpolestids have not previously been reported from the Bison Basin.

CM is the abbreviation used to designate specimens in the collections of the Section of Vertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. Measurements of tooth length (L) and width (W) follow those of Rose (1975:fig. 1).

#### SYSTEMATIC PALEONTOLOGY

- Class Mammalia Linnaeus, 1758  
 Mirorder Primatomorpha Beard, 1991  
 Superfamily Plesiadapoidea Trouessart, 1897  
 Family Carpolestidae Simpson, 1935  
 Subfamily Carpolestinae Simpson, 1935  
*Carpocristes* Beard and Wang, 1995  
*Carpocristes rosei*, **new species**  
 (Fig. 1)

*Holotype*.—CM 40567, left dentary fragment preserving the crowns of P<sub>4</sub>-M<sub>3</sub> and the complete or partial alveoli for several anterior teeth; only known specimen (Fig. 1).

*Type Locality*.—Bison Basin Ridge locality, CM loc. 1035. Geographic and stratigraphic data for this locality, on file in the Section of Vertebrate Paleontology (CM), indicate that this is the same locality Gazin (1956) referred to as the Ledge locality. The mammalian fauna from the Bison Basin Ledge locality correlates with middle Tiffanian zone Ti3 (Archibald et al., 1987).

*Known Distribution*.—Middle Tiffanian (Ti3) of the Bison Basin, Fremont County, south-central Wyoming.

*Diagnosis*.—P<sub>4</sub> differs from that of other species of *Carpocristes* in being relatively taller and anteroposteriorly shorter, with larger ultimate apical cusp, only minor posterolingual excavation, and weaker crest uniting main shearing blade with talonid cusp. M<sub>1</sub> trigonid cusps less widely splayed than in other species of *Carpocristes*. P<sub>4</sub> further differs from that of *Carpocristes hobackensis*, *Carpodectes*, and *Carpolestes* in being absolutely shorter anteroposteriorly. P<sub>4</sub> further differs from that of *Carpolestes*, *Carpocristes hobackensis*, and *Carpocristes oriens* in having fewer apical cusps. P<sub>4</sub> further differs from that of *Carpodectes* in having ultimate apical cusp displaced posteroinferiorly.

*Etymology*.—For Kenneth D. Rose, whose monograph on the Carpolestidae (Rose, 1975) remains a standard reference for the group.

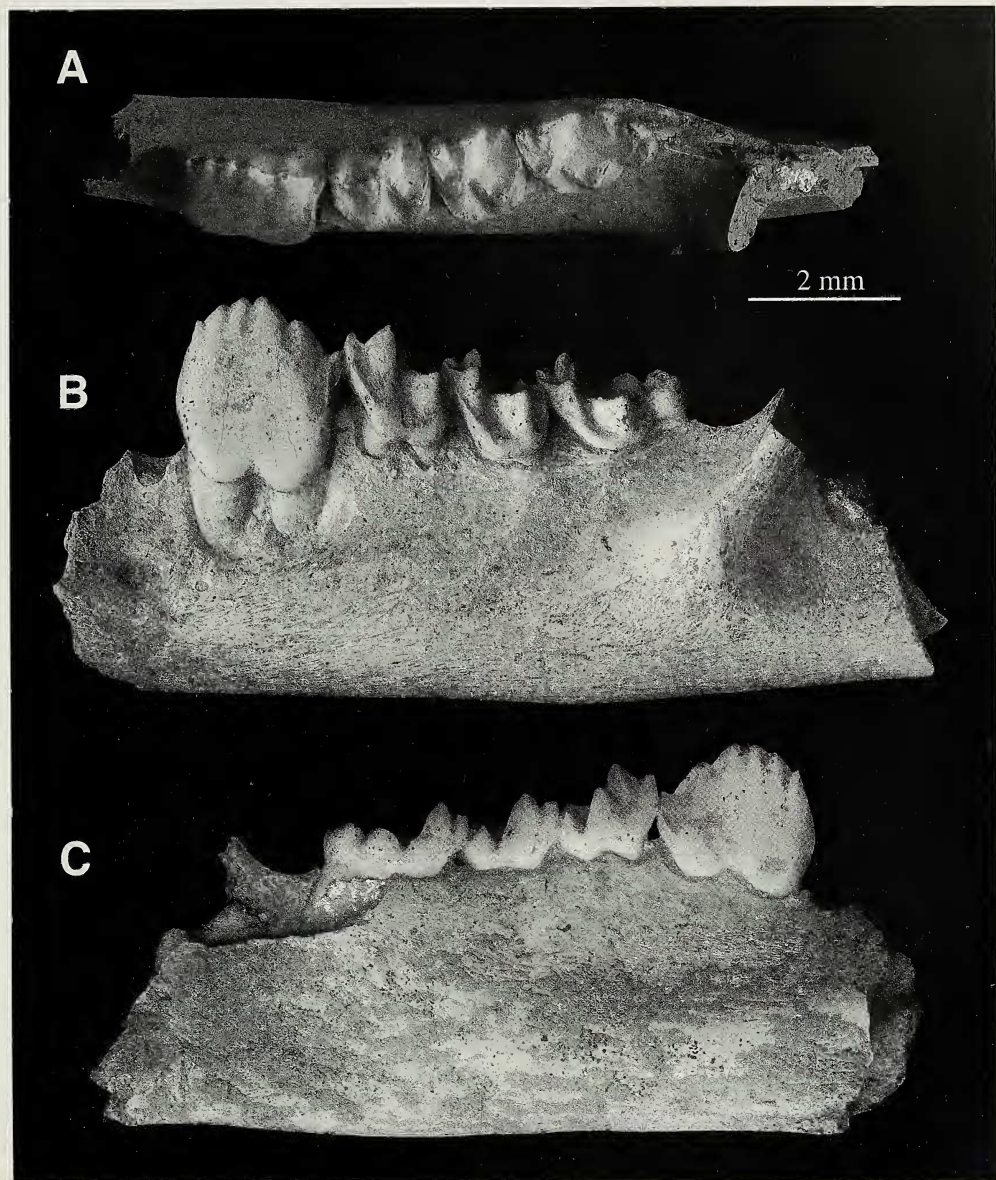


Fig. 1.—*Carpocristes rosei*, n. sp., holotype, CM 40567. Left dentary fragment preserving  $P_4$ - $M_3$  and whole or partial alveoli for anterior teeth in occlusal (A), buccal (B), and lingual (C) views. Note prominent region of alveolar bone resorption beneath  $P_4$  in buccal view (B). Scale bar = 2 mm.

*Description*.—Anteriorly, the posterior part of the alveolus for  $I_1$  is preserved in CM 40567. This relatively large alveolus is nearly horizontal in orientation, reflecting the procumbent disposition of  $I_1$  in carpolestids. At least two small alveoli are present between the crown of  $P_4$  and the alveolus for  $I_1$ , although this part of the dentary is damaged in the holotype. The more posterior of these two alveoli supported a diminutive, single-rooted  $P_3$  by analogy with other carpolestid taxa in which the crown of this tooth is preserved (Rose, 1975; Beard and Wang, 1995). The more anterior alveolus, of which only the posterior part is preserved in CM 40567, must have housed another single-rooted tooth that was similar in size to  $P_3$ . The homology of the latter tooth locus is uncertain given the fragmentary

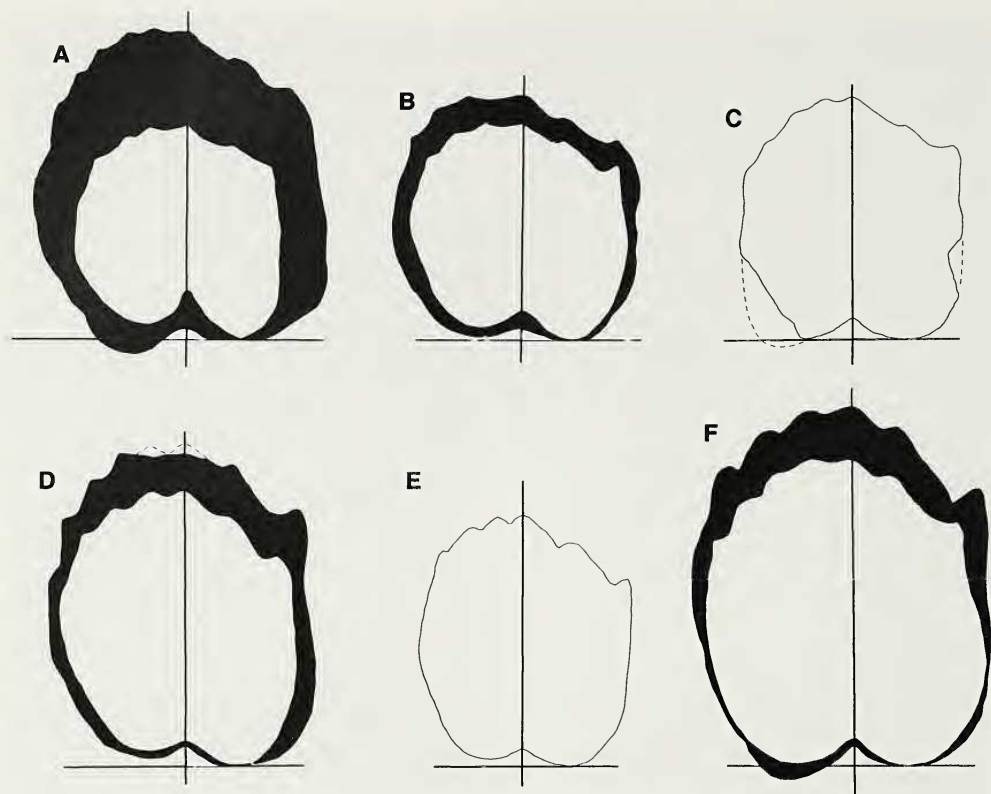


Fig. 2.—Camera lucida tracings of the labial profiles of  $P_4$  among selected Carpolestinae (after Krause, 1978:fig. 7). Samples depicted are as follows: (A) *Carpocristes cygneus*, Roche Percée local fauna,  $n = 19$ ; (B) *Carpocristes cygneus*, Swan Hills site 1,  $n = 4$ ; (C) *Carpocristes hobackensis*, Dell Creek Quarry,  $n = 1$ ; (D) *Carpocristes* sp., Police Point local fauna,  $n = 3$ ; (E) *Carpocristes rosei*, Bison Basin Ridge locality,  $n = 1$ ; (F) *Carpodaptes hazelae*, Scarritt Quarry and Cedar Point Quarry,  $n = 2$ .

nature of the only known specimen of *C. rosei*, but it must have been either  $C_1$  or  $P_2$ . That which is preserved of the anterior part of the dentary in CM 40567 does not differ appreciably from comparable parts of the dentary in *Carpodaptes hazelae* and *Carpocristes cygneus*.

The most noteworthy feature on the labial aspect of the dentary is a prominent area of missing bone beneath the crown of  $P_4$ , which may have been due to pathology.

The labial profile of  $P_4$  (L, 2.00 mm; W, 1.30 mm) closely resembles that of *Carpodaptes hazelae*, from which it differs primarily in being smaller and in the placement of the ultimate apical cusp (Fig. 2).  $P_4$  in *Carpocristes rosei* is relatively taller and anteroposteriorly shorter than in other species of *Carpocristes*. Five apical cusps are present, which is fewer than occur on  $P_4$  in *Carpocristes oriens* ( $n = 7$ ; Beard and Wang, 1995), and at the low end of the range for *Carpocristes cygneus* ( $n = 5-7$ , mode = 6; Krause, 1978). In contrast to its more anterior position in *Carpodaptes*, in *Carpocristes rosei* the ultimate apical cusp is located almost equidistant between the talonid cusp and the penultimate apical cusp. This posteroinferior displacement of the ultimate apical cusp is a diagnostic apomorphy for *Carpocristes* (Beard and Wang, 1995:fig. 14). In *C. rosei* the ultimate apical cusp is large and cuspidate, in contrast to the condition in other species of *Carpocristes*, in which this cusp is smaller and less readily distinguished from the crest that unites the talonid cusp with the remainder of the  $P_4$  blade. The latter crest itself is decidedly weaker in *C. rosei* than in other species of *Carpocristes*, which is a second reason that the ultimate apical cusp is so manifest in *C. rosei*. Lingually, vertical ribs are well developed beneath all of the apical cusps of  $P_4$ . The posterolingual part of the crown is only weakly excavated. As a result, the anterior apical cusps are located almost directly

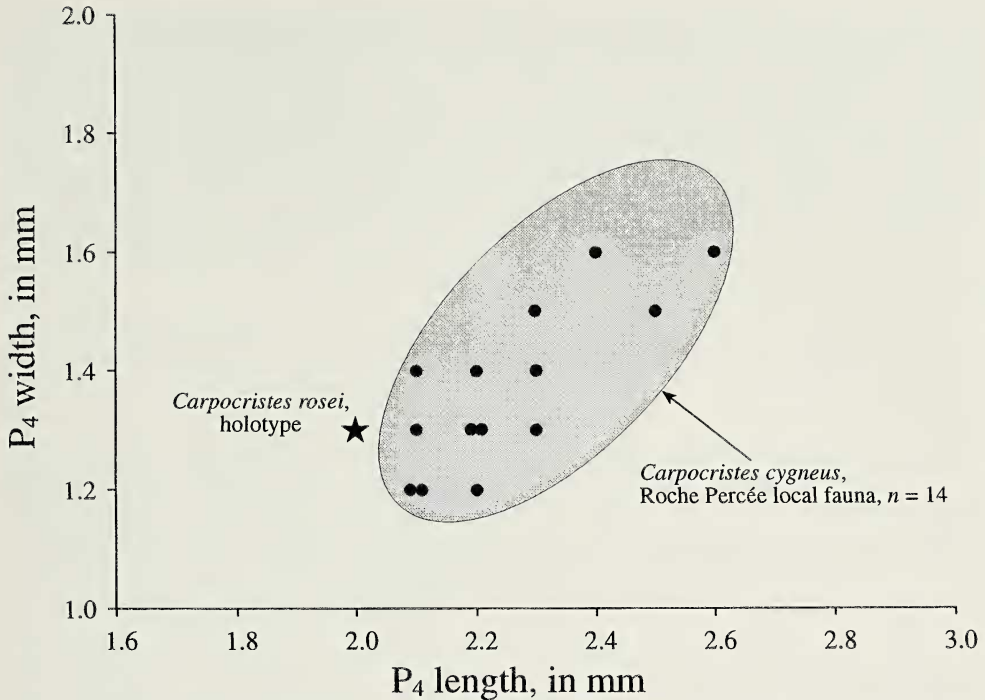


Fig. 3.—Bivariate plot of  $P_4$  dimensions in the holotype of *Carpodactes rosei* (CM 40567) and a sample of *Carpodactes cygneus* from the Roche Percée local fauna of Saskatchewan [*C. cygneus* data from Krause (1978:table 2)].

anterior to the ultimate apical cusp, rather than being tilted or displaced lingually with respect to the ultimate apical cusp, as is the case in other species of *Carpodactes*.

The lower molars of *C. rosei* differ little from those of other species of *Carpodactes*, and need not be described in detail here. In *C. rosei* the paraconid and metaconid cusps on  $M_1$  are less widely splayed than is the case in other species of *Carpodactes*. Unlike *C. hobackensis*, there is no development of a lingual cingulid on the trigonid of  $M_1$  in *C. rosei*. In general, the lower molar cusps in all species of *Carpodactes* seem to be less inflated and bear better-developed crests than do their homologues in *Carpodactes* and *Carpolestes*. Measurements of the lower molars in CM 40567 are as follows:  $M_1$  L, 1.20 mm;  $M_1$  W, 1.20 mm;  $M_2$  L, 1.10 mm;  $M_2$  W, 1.25 mm;  $M_3$  L, 1.80 mm;  $M_3$  W, 1.10 mm.

**Discussion.**—*Carpodactes rosei* is most easily confused with *Carpodactes cygneus*, which is closely related to the new form. However, extensive comparisons between the holotype of *C. rosei* and casts of specimens of *C. cygneus* from the Roche Percée local fauna of Saskatchewan described by Krause (1978) revealed consistent morphological differences, which are summarized in the diagnosis.  $P_4$  in the holotype of *C. rosei* also falls outside the range of metric variation observed in the large sample of *C. cygneus* from Roche Percée (Fig. 3).

The most nearly complete and most reliably referred specimens of *C. cygneus* are derived from sites belonging to late Tiffanian zone Ti4. While these late Tiffanian specimens differ from the holotype of *C. rosei* in ways that support a species-level distinction, fossils from various middle Tiffanian (Ti3) sites that have previously been referred to *C. cygneus* appear to be more problematic. Some or even all of these specimens may ultimately prove to belong to *C. rosei* rather

than to *C. cygneus*. For example, based on published descriptions and illustrations (Krishtalka, 1973:fig. 16; Krause, 1978:fig. 7), the carpolesiid from the Police Point local fauna of southeastern Alberta is very similar to *C. rosei*, and these specimens may well document a northern range extension for this species (Fig. 2). Likewise, it is possible that middle Tiffanian specimens from localities along the Blindman River in central Alberta referred by Fox (1990) to *C. cygneus* pertain to *C. rosei* instead. However, the latter specimens have yet to be described or illustrated, so that their species-level attribution remains uncertain. Finally, specimens from the Williston Basin of western North Dakota referred by Holtzman (1978) to *C. cygneus* may instead belong to *C. rosei*.

CARPOLESTID PHYLOGENY AND THE PHYLOGENETIC POSITION OF  
*CARPOCRISTES ROSEI*

*Introduction*

The broad outlines of carpolesiid phylogeny have been established for at least a quarter of a century, when Rose (1975) published his monograph on the group. Relationships among generic-level taxa of North American carpolesiids have remained stable throughout this interval, although the affinities of two Asian genera have proven to be somewhat more controversial (Beard and Wang, 1995; Bloch and Gingerich, 1998). Despite this virtual consensus at the generic level, certain species-level relationships within the group have so far defied resolution. For example, there is little or no consensus regarding which of the four described species of *Elphidotarsius* is most closely related to the clade that includes *Carpodaptus*, *Carpocristes*, and *Carpolestes*, despite virtual unanimity regarding the paraphyly of *Elphidotarsius* (Rose, 1975; Krause, 1978; Fox, 1984). Similarly, the affinities of both *Carpolestes* and *Carpocristes* with respect to the phylogenetically more basal species traditionally included in *Carpodaptus* have yet to be resolved satisfactorily, although *Carpodaptus jepseni* is often cited as being closely related to *Carpolestes* (Rose, 1975; Bloch and Gingerich, 1998). Various workers have entertained the possibility that *Carpolestes* and some or all of the species now included in *Carpocristes* are more closely related to each other than either are to *Carpodaptus* (Dorr, 1952; Rose, 1975; Krause, 1978). However, this conclusion conflicts with the phylogeny published by Beard and Wang (1995:fig. 14), in which a relatively basal dichotomy between *Carpocristes* and *Carpolestes* was inferred, with both *Carpodaptus hazelae* and *Carpodaptus jepseni* being more closely allied to *Carpolestes* than to *Carpocristes*. A major obstacle to resolution of these lower-level relationships among carpolesiids is our poor knowledge of the anatomy of many of the relevant taxa, which are often documented by unique or extremely fragmentary specimens.

*Methods*

In an attempt to clarify these details of carpolesiid phylogeny, I extended the taxon-character matrix published by Beard and Wang (1995:appendices 1, 2) to include additional dental characters and all known carpolesiid species (Appendices 1, 2). Multistate characters were treated as ordered in cases in which convincing evidence for a morphocline exists. For example, the number of apical cusps on P<sub>4</sub>, which varies from two to eight among carpolesiids, was treated as an ordered character on the assumption that the number of apical cusps on P<sub>4</sub> evolved consecutively rather than randomly. Likewise, certain other characters were treated

as irreversible when, as in the case of the presence or absence of a particular tooth locus, evolutionary reversal seems highly implausible. All character state transformations were weighted equally. Details regarding character status are provided in Appendix 1. Trees were rooted by designating *Pronothodectes matthewi*, *Chronolestes simul*, and a hypothetical ancestor as outgroups to carpolestine taxa. Phylogenetic analysis of this enhanced dataset using PAUP 3.1.1 (Swofford, 1993) yielded nine most parsimonious trees, a strict consensus of which is illustrated in Figure 4.

### Results

The topology of the strict consensus tree (Fig. 4) is fully consistent with that published by Beard and Wang (1995:fig. 14), although additional taxa are included here. As has long been assumed, *Elphidotarsius* emerges as a highly paraphyletic assemblage of species that successively approximates more derived carpolestids (Fig. 4, nodes 2-4). Both *E. shotgunensis* and *E. russelli* appear to be more closely related to the *Carpodaptus* + *Carpocristes* + *Carpolestes* clade than is either *E. florencae* or *E. wightoni* (Fig. 4, node 4). However, neither of the former species of *Elphidotarsius* is represented by relatively complete material, and their derived  $P_4$  structure forms the only unambiguous character support presently available for the phylogenetic relationships reconstructed here. More nearly complete material of either or both of these species will be necessary to evaluate their affinities adequately. As originally proposed by Fox (1984), *E. wightoni* appears to be related more closely to the *Carpodaptus* + *Carpocristes* + *Carpolestes* clade than is *E. florencae* (Fig. 4, node 3).

Among more advanced carpolestids (Fig. 4, node 5), a fundamental dichotomy appears to define two basic clades. One of these clades is equivalent to the genus *Carpocristes* (Fig. 4, node 6), the most basal species of which is *Carpocristes rosei*. Relationships among more advanced species of *Carpocristes* are the same as those proposed by Beard and Wang (1995). That is, *Carpocristes cygneus* appears to be the sister group of a clade consisting of *Carpocristes hobackensis* and *Carpocristes oriens* (Fig. 4, nodes 7, 8). The sister group of *Carpocristes* appears to be a clade that includes both *Carpodaptus* and *Carpolestes*.

The phylogenetic position of *Carpodaptus hazelae*, inferred here to be the sister group of all other species of *Carpodaptus* and *Carpolestes* (Fig. 4, node 9), is the weakest node on the consensus tree. This node occurs in only 35% of bootstrapped trees, and is supported by a single character transformation (the loss of  $P_2$ , which occurred four times in parallel within Carpolestidae according to the character walk optimized here). Regardless of the affinities of *Carpodaptus hazelae*, and despite Beard and Wang's (1995) transfer of *C. cygneus* and *C. hobackensis* (both formerly included in *Carpodaptus*) to *Carpocristes*, *Carpodaptus* continues to emerge as a paraphyletic group of species that successively approximates *Carpolestes*. The type species of *Carpodaptus*, *C. aulacodon*, appears to be the sister group of a clade that includes *Carpodaptus jepseni* and *Carpolestes* (Fig. 4, nodes 10, 11). Relationships among species of *Carpolestes* agree with those recently proposed by Bloch and Gingerich (1998): *C. dubius* appears to be the sister group of a clade that consists of *C. nigridens* and *C. simpsoni* (Fig. 4, nodes 12, 13).

### Discussion

Perhaps the most notable result from the phylogenetic analysis of carpolestids performed here is the cohesion of the *Carpocristes* clade with respect to other

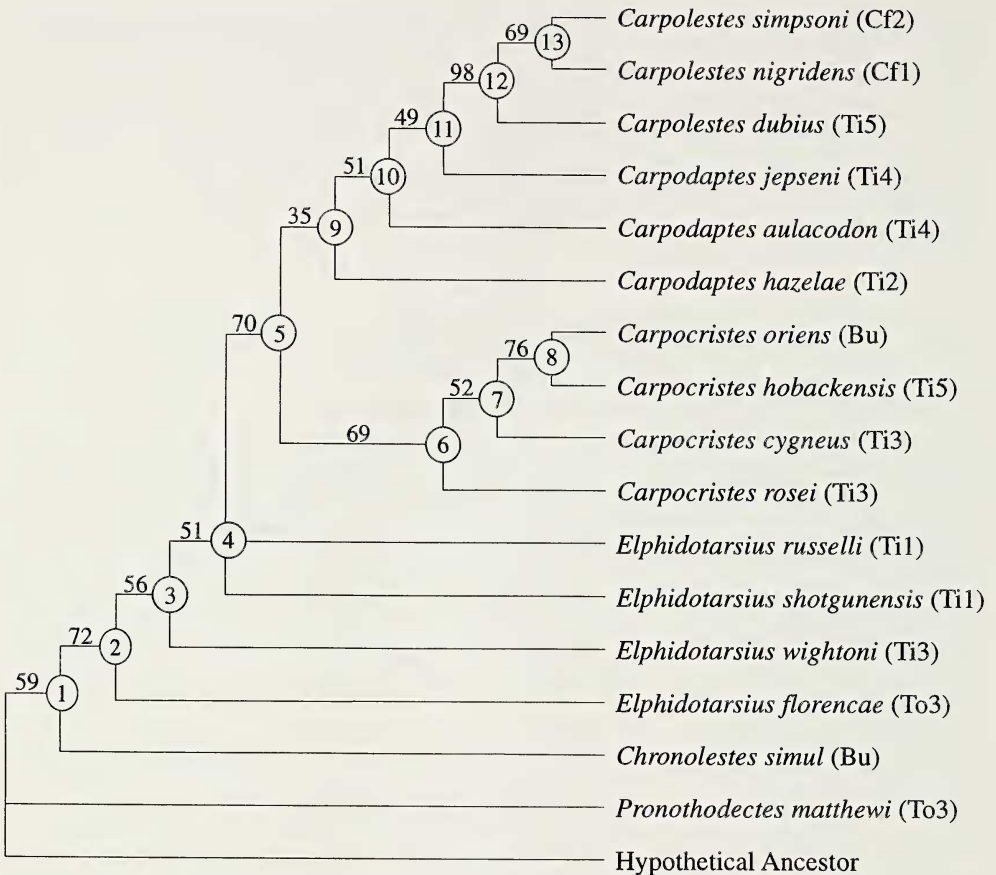


Fig. 4.—Strict consensus of nine most parsimonious trees recovered from branch-and-bound search in PAUP 3.1.1 (Swofford, 1993) of character-taxon matrix given in Appendix 2. For details regarding character status, see Appendix 1. Tree length = 75; consistency index (excluding uninformative characters) = 0.757. Numerical values above stems of clades indicate percent frequency with which those clades were supported in 100 bootstrapped trees. Earliest known stratigraphic occurrence of each species is given in parentheses. For details regarding stratigraphic occurrence and estimated antiquity of each species, see Appendix 3.

Using the ACCTRAN character-state optimization algorithm, synapomorphies supporting each node are as follows (see Appendix 1 for description of character states): Node 1 (Carpolestidae), Character 14 (0→1), Character 25 (0→1), Character 32 (0→1), Character 37 (0→1), Character 38 (0→1), Character 41 (0→1); Node 2 (Carpolestinae), Character 3 (0→1), Character 4 (0→1), Character 9 (0→1), Character 16 (0→1), Character 18 (0→1), Character 19 (0→1), Character 20 (0→1), Character 26 (0→1), Character 32 (1→3), Character 39 (0→1), Character 42 (0→1); Node 3, Character 5 (0→1), Character 6 (0→1), Character 11 (0→1), Character 12 (1→2), Character 40 (0→1); Node 4, Character 5 (1→2), Character 7 (1→2), Character 13 (1→2), Character 17 (0→1), Character 33 (0→1), Character 34 (0→1); Node 5, Character 22 (0→1), Character 24 (0→1), Character 32 (3→4); Node 6 (*Carpocristes*), Character 10 (0→1), Character 15 (0→1), Character 21 (0→1), Character 35 (0→1), Character 36 (0→1); Node 7, Character 32 (4→5); Node 8, Character 7 (2→3), Character 8 (0→1), Character 10 (1→2), Character 15 (1→2), Character 27 (0→1), Character 28 (0→1), Character 31 (0→1); Node 9, Character 23 (0→1); Node 10, Character 6 (1→2), Character 8 (0→1), Character 29 (0→1); Node 11, Character 32 (4→5); Node 12 (*Carpolestes*), Character 27 (0→1), Character 28 (0→1), Character 30 (0→1), Character 32 (5→7); Node 13, Character 8 (1→2).



advanced carpolestids. This supports the recognition of *Carpocristes* as a genus distinct from *Carpodaptus*, all species of which appear to share more recent common ancestry with *Carpolestes* than with *Carpocristes*. Given the phylogenetic relationships depicted in Figure 4, cladogenesis between *Carpocristes* and other carpolestids must have occurred sometime prior to the late early Tiffanian (Ti2). This inference is based on the earliest known occurrence of the *Carpodaptus* + *Carpolestes* clade, which is provided by *Carpodaptus hazelae* at Scarritt Quarry in the Crazy Mountains Basin of south-central Montana. All species of *Carpocristes* other than *C. oriens* are restricted to North America. Both phylogenetic and biostratigraphic data therefore imply that *Carpocristes* originated in North America prior to dispersing to Asia sometime during the late Paleocene (Beard and Wang, 1995; Beard, 1998).

In general, there is marked agreement between the tree topology depicted in Figure 4 and the stratigraphic ranges of carpolestid species. This can be quantified using Huelsenbeck's (1994) stratigraphic consistency index (SCI), which is the proportion of internal nodes on a cladogram that are consistent with the stratigraphic distributions of sister taxa divided by the total number of internal nodes. Of the 13 internal nodes in Figure 4, ten are consistent with the stratigraphic distributions of sister taxa, yielding an SCI of 0.769. Estimates of ghost lineage durations for the stratigraphically inconsistent nodes are based on correlation of Paleocene mammal-bearing strata from the Western Interior of North America with the Geomagnetic Polarity Time Scale (Butler et al., 1981, 1987; Berggren et al., 1995) and biostratigraphic correlations between North America and Asia proposed by Beard and Dawson (1999) (Appendix 3). The longest ghost lineage implied by the phylogeny depicted in Figure 4 and the stratigraphic distribution of carpolestid species is that between *Chronolestes* and Carpolestinae. The duration of this ghost lineage is equivalent to the difference between the earliest known occurrence of a carpolestine (provided by *Elphidotarsius florencae* in zone To3, estimated at 61.4 Ma) and the much younger occurrence of *Chronolestes* (Bumbanian, estimated at 55.8 Ma), which is roughly 5.6 Ma. A shorter ghost lineage of about 2.3 Ma duration separates the anachronistically young *Elphidotarsius wightoni* (zone Ti3, estimated at 58.3 Ma) from the earliest known occurrence of its sister taxon (zone Ti1, estimated at 60.6 Ma). In contrast, the duration of the ghost lineage implied by the earliest known occurrences of *Carpocristes* (Ti3, estimated at 58.3 Ma) and the *Carpodaptus* + *Carpolestes* clade (Ti2, estimated at 59.5 Ma) is only about 1.2 Ma.

Despite the stratigraphically dense succession of carpolestids known from Paleocene basins in western North America, significant episodes of their evolutionary history remain undocumented by the fossil record. The documentation of incompatibility between robust phylogenetic trees and the stratigraphic distributions of individual taxa is a useful endeavor because it highlights these elusive episodes of evolutionary history, thereby providing a guide to fertile areas of future research.

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## APPENDIX 1

*Character Descriptions, with Character Status in Italics*

1. Laterocone or disto-apical cusp on I<sup>1</sup>: absent (0); or present (1).
2. Mediocone on I<sup>1</sup>: absent (0); or present (1).
3. Mesio-basal cusp on I<sup>1</sup>: absent (0); or present (1).
4. Lingual crest on P<sup>3</sup>: absent (0); or present (1).
5. Number of cusps on lingual crest of P<sup>3</sup>: none (0); one (1); or two (2) (*ordered*).
6. Parastyle on P<sup>3</sup>: absent (0); present (1); or present, with neomorphic cusp anterior to it (2) (*ordered*).
7. Number of buccal cusps posterior to paracone on P<sup>3</sup>: none (0); one (1); two (2); or three (3) (*ordered*).
8. Parastylar lobe on P<sup>3</sup>: does not project anteriorly with respect to lingual part of tooth (0); moderate anterior projection (1); or extreme anterior projection (2) (*ordered*).
9. Median crest on P<sup>3</sup>: absent (0); or present (1).
10. Number of median crests on P<sup>3</sup>: one (0); two (1); or three (2) (*ordered*).
11. Position of primary median crest on P<sup>3</sup>: lingual, closely appressed to lingual crest (0); or labial, widely separated from lingual crest (1).
12. Parastyle on P<sup>4</sup>: absent (0); present, single (1); or present, dual (2) (*ordered*).
13. Number of buccal cusps posterior to paracone on P<sup>4</sup>: none (0); one (1); or two (2) (*ordered*).
14. Median crest on P<sup>4</sup>: absent (0); or present (1).
15. Number of median crests on P<sup>4</sup>: one (0); two (1); or three (2) (*ordered*).
16. Position of protocone on P<sup>4</sup>: anterior (0); or central (1).
17. Number of lingual cusps on P<sup>4</sup>: one (0); or three (1).
18. Crest running anterior to paracone on P<sup>4</sup>: absent (0); or present (1).
19. Position of paraconule on P<sup>4</sup>: anterior (0); or central (1).
20. Postparaconule crista on P<sup>4</sup>: incomplete (0); or complete (1).
21. Size of upper and lower molars: larger than in *Carpocristes* spp. (0); or as in *Carpocristes* spp. (1).
22. I<sub>3</sub>: present (0); or absent (1) (*irreversible*).
23. P<sub>2</sub>: present (0); or absent (1) (*irreversible*).
24. P<sub>3</sub>: double-rooted (0); or single-rooted (1) (*irreversible*).
25. Size of P<sub>3</sub>: unreduced (0); or reduced or absent (1) (*irreversible*).
26. Plagiaulacoid P<sub>4</sub>: absent (0); or present (1).
27. Vertical rib beneath ultimate apical cusp on lingual side of P<sub>4</sub>: present (0); or absent (1).
28. Crest uniting penultimate apical cusp with talonid cusp on P<sub>4</sub>: weak (0); or strong (1).
29. Vertical ribs beneath anterior apical cusps on lingual side of P<sub>4</sub>: vertically oriented (0); or steeply inclined from base of tooth anteriorly to apical cusps posteriorly.

30. Position of  $P_4$  talonid cusp: well below the level of  $M_1$  trigonid (0); or elevated to near the level of  $M_1$  trigonid (1).

31. Ultimate apical cusp on  $P_4$ : cuspsate (0); or indistinct or absent, being incorporated within crest uniting main shearing blade of  $P_4$  with talonid cusp (1).

32. Number of apical cusps on  $P_4$ : one (0); two (1); three (2); four (3); five (4); six (5); seven (6); or eight (7) (*ordered*).

33. Position of ultimate apical cusp (= metaconid) on  $P_4$ : slightly to moderately lingual to penultimate apical cusp (0); or directly posterior to it (1).

34. Position of apical cusps immediately preceding penultimate apical cusp (= protoconid) on  $P_4$ : slightly to moderately lingual to penultimate apical cusp (0); or directly anterior to it (1).

35. Position of ultimate apical cusp on  $P_4$ : near penultimate apical cusp (0); or more posterior in position, roughly equidistant between penultimate apical cusp and talonid cusp (1).

36. Posterolingual excavation on  $P_4$ : absent (0); or present (1).

37. Anteroposterior elongation of  $P_4$ : absent (0); or present (1).

38. Exodaenodonty on  $P_4$ : absent (0); or present (1).

39. Paraconid of  $M_1$ : not widely splayed relative to metaconid (0); or widely splayed (1).

40. Talonid notch on  $M_1$ : weak to absent (0); or strong (1).

41. Protoconid of  $M_1$ : same height as paraconid and metaconid (0); or taller than paraconid and metaconid (1).

42. Talonid of  $M_1$ : similar in anteroposterior length to that of  $M_2$  (0); anteroposteriorly abbreviated (1).

## APPENDIX 2

Taxon-Character Matrix Used in Parsimony Analysis

Hypothetical Ancestor	0000?	00?0?	?000?	00000	00000	0???0	?0????	00000	00
<i>Pronothodectes matthewi</i>	1100?	01?0?	?110?	00000	01000	0???0	?0????	00000	00
<i>Chronolestes simul</i>	0000?	00?0?	?0010	00000	01011	000?0	010?0	01100	10
<i>Elphidotarsius florenceae</i>	???10	01?10	01110	10111	01001	10000	03000	01110	11
<i>Elphidotarsius wightoni</i>	???11	11010	12110	10111	011?1	10000	03000	01111	11
<i>Elphidotarsius russelli</i>	?????	?????	?????	?????	0????	10000	03110	011??	??
<i>Elphidotarsius shotgunensis</i>	?????	?????	?????	?????	000?1	10000	03110	01111	11
<i>Carpodaptes hazelae</i>	11112	12010	12210	11111	01111	10000	04110	01111	11
<i>Carpodaptes aulacodon</i>	?????	?????	?????	?????	0??11	10010	04110	01111	11
<i>Carpodaptes jepseni</i>	?????	?????	?????	?????	0????	10010	05110	01111	11
<i>Carpolestes dubius</i>	???12	22110	12210	11111	01111	11111	07110	01111	11
<i>Carpolestes nigridentis</i>	10112	22210	12210	11111	01111	11111	07110	01111	11
<i>Carpolestes simpsoni</i>	10112	22210	12210	11111	011?1	11111	07110	01111	11
<i>Carpocristes rosei</i>	?????	?????	?????	?????	1???1	10000	04111	11111	11
<i>Carpocristes cygneus</i>	10112	12011	12211	11111	111?1	10000	05111	11111	11
<i>Carpocristes hobackensis</i>	?????	?????	?????	?????	11111	11100	15111	11111	11
<i>Carpocristes oriens</i>	???12	13112	12212	11111	110?1	11100	16111	11111	11

## APPENDIX 3

### *Explanatory Notes for the Age Estimates Used Here for Carpolestids and Related Taxa, based on Biostratigraphy and Paleomagnetic Stratigraphy*

*Pronothodectes matthewi*: Gidley Quarry, Crazy Mountains Basin, MT (To3). Assigned to upper part of Chron 27r, based on paleomagnetic data from Silberling Quarry, Crazy Mountains Basin and Rock Bench Quarry, Bighorn Basin (Butler et al., 1987). Absolute age estimated at 61.4 Ma (Berggren et al., 1995).

*Chronolestes simul*: Wutu Formation, Shandong Province, People's Republic of China (Bumbanian). Estimated to correlate with North American zone Cf2 based on biostratigraphy (Beard and Dawson,

1999). Assigned to lowest part of Chron 24r, based on paleomagnetic data from the Bighorn Basin (Butler et al., 1981). Absolute age estimated at 55.8 Ma (Berggren et al., 1995).

*Elphidotarsius florencae*: Gidley Quarry, Crazy Mountains Basin, MT; Rock Bench Quarry, Bighorn Basin, WY (To3). Assigned to upper part of Chron 27r, based on paleomagnetic data from Silberling Quarry, Crazy Mountains Basin and Rock Bench Quarry, Bighorn Basin (Butler et al., 1987). Absolute age estimated at 61.4 Ma (Berggren et al., 1995).

*Elphidotarsius wightoni*: University of Alberta localities DW-1 and DW-2, near Red Deer, Alberta (Ti3). Fossils possibly pertaining to this species were cited by Fox (1990:59) from Aaron's Locality (Ti1 or Ti2), but the stratigraphic range for the species is not extended here, pending formal description of the relevant specimens. Assigned to upper part of Chron 26r, based on paleomagnetic data from the Crazy Mountains Basin and Bighorn Basin (Butler et al., 1981, 1987). Absolute age estimated at 58.3 Ma (Berggren et al., 1995).

*Elphidotarsius shotgunensis*: Keefer Hill local fauna (= Shotgun local fauna), Wind River Basin, WY (Ti1). Assigned to lower part of Chron 26r, based on paleomagnetic data from the Crazy Mountains Basin and Bighorn Basin (Butler et al., 1981, 1987). Absolute age estimated at 60.6 Ma (Berggren et al., 1995).

*Elphidotarsius russelli*: Cochrane 2 locality, Porcupine Hills Formation, Alberta (Ti1). Assigned to lower part of Chron 26r, based on paleomagnetic data from the Crazy Mountains Basin and Bighorn Basin (Butler et al., 1981, 1987). Absolute age estimated at 60.6 Ma (Berggren et al., 1995).

*Carpocristes rosei*: Ridge locality [= Ledge locality of Gazin (1956)], Bison Basin, WY (Ti3). Assigned to upper part of Chron 26r, based on paleomagnetic data from the Crazy Mountains Basin and Bighorn Basin (Butler et al., 1981, 1987). Absolute age estimated at 58.3 Ma (Berggren et al., 1995).

*Carpocristes cygneus*: Swan Hills site 1, Alberta; Canyon Ski Quarry, Alberta; Roche Percée local fauna, Saskatchewan (Ti4). Several possible records from zone Ti3 (e.g., from University of Alberta locality DW-1 near Red Deer, Alberta; Police Point local fauna, Alberta) have been listed by Fox (1990). Additional specimens from the Judson and Brisbane localities in western North Dakota (Ti3) may also pertain to *C. cygneus*. Although the best samples of this species are known from Ti4 sites, the earliest known records of *C. cygneus* are provisionally considered to be Ti3. Assigned to upper part of Chron 26r, based on paleomagnetic data from the Crazy Mountains Basin and Bighorn Basin (Butler et al., 1981, 1987). Absolute age estimated at 58.3 Ma (Berggren et al., 1995).

*Carpocristes hobackensis*: Dell Creek Quarry, Hoback Basin, WY (Ti5). Assigned to middle part of Chron 25r based on paleomagnetic data from the Bighorn Basin, WY (Butler et al., 1981). Absolute age estimated at 57.0 Ma (Berggren et al., 1995).

*Carpocristes oriens*: Wutu Formation, Shandong Province, People's Republic of China (Bumbanian). Estimated to correlate with North American zone Cf2 based on biostratigraphy (Beard and Dawson, 1999). Assigned to lowest part of Chron 24r, based on paleomagnetic data from the Bighorn Basin (Butler et al., 1981). Absolute age estimated at 55.8 Ma (Berggren et al., 1995).

*Carpodartes hazelae*: Scarritt Quarry, Crazy Mountains Basin, MT (Ti2); Cedar Point Quarry, Bighorn Basin, WY (Ti3); Hand Hills West locality, Alberta (Ti3); various localities in the Paskapoo Formation along the Blindman River near Red Deer, Alberta (Ti3); Joffe Bridge Roadcut, lower level, Alberta (Ti3). Earlier specimens that may pertain to this species are known from the Keefer Hill local fauna of the Wind River Basin, WY (Ti1) and from the Cochrane 2 site in Alberta (Ti1). However, pending fuller description of these specimens, the earliest reliable occurrence of *C. hazelae* is here regarded as Ti2. Assigned to the middle part of Chron 26r, based on paleomagnetic data from Scarritt Quarry, MT (Butler et al., 1987). Absolute age estimated at 59.5 Ma (Berggren et al., 1995).

*Carpodartes aulacodon*: Mason Pocket locality, Animas Formation, San Juan Basin, CO (Ti4). Assigned to lower part of Chron 25r, based on paleomagnetic data from the local section (Butler et al., 1981). Absolute age estimated at 57.4 Ma (Berggren et al., 1995).

*Carpodartes jepseni*: Divide Quarry, Bighorn Basin, WY (Ti4). Assigned to lower part of Chron 25r,

based on paleomagnetic data from the Bighorn Basin (Butler et al., 1981). Absolute age estimated at 57.4 Ma (Berggren et al., 1995).

*Carpolestes dubius*: Princeton Quarry and nearby sites, Bighorn Basin, WY (Ti5). Assigned to middle part of Chron 25r based on paleomagnetic data from the Bighorn Basin, WY (Butler et al., 1981). Absolute age estimated at 57.0 Ma (Berggren et al., 1995).

*Carpolestes nigridentis*: Bear Creek locality, northern Bighorn Basin, MT (Cf1); Big Multi Quarry, Washakie Basin, WY (Cf1). Assigned to early part of Chron 25n based on paleomagnetic data from the Bighorn Basin, WY (Butler et al., 1981). Absolute age estimated at 56.3 Ma (Berggren et al., 1995).

*Carpolestes simpsoni*: various localities in the northern Bighorn Basin, WY (Cf2-Cf3). Assigned to lowest part of Chron 24r, based on paleomagnetic data from the Bighorn Basin (Butler et al., 1981). Absolute age estimated at 55.8 Ma (Berggren et al., 1995).